which are more or less arbitrary and unsatisfactory, and all of which are liable to be set aside at any time. I have here adopted Migula's system[22] which seems to me very convenient, and on the whole the most satisfactory of any that has yet appeared.

Before proceeding to the body of this review it only remains to say that every effort has been made to deal impartially with the material in hand, and to present the essential ideas of the writers as concisely and accurately as possible. To this end the original papers have been consulted in every instance, unless otherwise stated in the text. So much vexation over wrong references has been experienced in time past by the writer that he has himself been at special pains to give full and accurate citations. It is to be hoped, therefore, that the reader will have no difficulty in finding the original papers. An endeavor has also been made to bring the subject fully up to date but it is quite likely that some worthy papers may have been overlooked, owing to the many languages and the ever increasing number of places of publication.

# THE MEANING AND STRUCTURE OF THE SO-CALLED "MUSHROOM BODIES" OF THE HEXAPOD BRAIN.

By F. C. Kenyon, Ph. D.[1]

In looking at a series of sections of the brain of a hexapod, especially of a hymenopteron, the most notable structures are two pairs, one to each side, of large cup-shaped bodies of "Punkt substanz," or, what in the light of our present knowledge of nerve structure is better denominated fibrillar substance. Each of these cups is filled to overflowing with cells having large nuclei and very little cytoplasm. From the under surface

[22] Migula: Schizophyta: (22) Schizomycetes. *Die Natuerlichen Pflanzenfamilien* (Engler u. Prantl). I Teil. 1 Abt. a, Lief. 129. 8vo. p. 44, Leipzig, 1896. This is the forerunner of a larger work soon to be published by Gustav Fischer, Jena.

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each of these cups or "Becher" there descends into the general fibrillar substance of the brain a column of fibrillar substance which unites with its fellow of the same side to send a large branch obliquely downwards to the median line of the brain and an equally large or larger branch straight forwards to the anterior cerebellar surface. (Fig. B.)

Long before our present methods of sectioning and staining had found general application in the study of animal structure, or as early as 1850, the French naturalist, Dujardin, discovered these bodies in transparent preparations *in toto* of the brains of certain Hymenoptera and Orthoptera. From their somewhat folded appearance he describes them as "lobes à convolutiones," and compared them with the convolutions of the human brain, and even thought them associated with hexapod intelligence. Fourteen years later, Leydig, using the same methods confirmed Dujardin's discovery in working with the brains of the ant, bee, and wasp, and described them as "gestielter Körper." In 1875 Rabl-Rückhard identified the bodies in *Gryllus italicus*, *Locusta viridissima*, and *Dycticus verrucornis*, and correctly described the form of the "cup" under the term "Rind Körper." The very next year ('76) Dietl's application of the section method to the subject confirmed and perfected previous descriptions, and, struck with the resemblance to mushrooms, he adopted the name of "Pilzhutförmiger Körper," a conception later used by Packard (mushroom bodies) and by Bellocici ('82) (corpo fungiformo).

As to the intellectual function of the bodies, not all of the early writers supported Dujardin's inference. They were supposed to be connected with sight; but Rabl-Rückhard showed that they are fully developed in a blind African ant (Typhlopone). Dietl was loth to acknowledge an intellectual function, even though he found the organs more highly developed in Hymenoptera than in Orthoptera. But Forel ('74) adhered to Dujardin's supposition, and showed that among Hymenoptera even of the same species the bodies are most prominent where one usually recognizes most intelligence, as in the worker bees and ants, while they are small in the females and the males. Brandt ('76) two years later in a note on the brain of Hymen-

optera makes the same observations as to the differences in the same species, while Berger ('78) considered the structures as "organs of projection of the first order."

The supposition of Dujardin obtained its best support so far as the older methods would avail in the comprehensive work of Flögel ('78) covering the whole group of hexapods. Here, one may see at a glance that the development of the structures largely coincides with the development of intelligence, as shown by the following abridgement of his table:

| | |
|---|---|
| A. The four cups completely developed. | |
| 1. Very highly developed, | *Vespa.* |
| 2. Large with rim, | *Apis, Formica Pompilus, Ichneumonidæ.* |
| 3. Without rim, | *Blatta.* |
| 4. Very small, | *Cossus, Sphinx, Vanessa.* |
| B. Cups incomplete. | |
| 5. Walls and cells so reduced as hardly to be recognized as cups, | *Tenthredo, Cynips.* |
| 6. Reduced to two small heaps, | Many small butterflies. |
| 7. Wall a broad plate, | *Forficula, Acridium,* etc. |
| 8. Wall (fibrillar substance) absent. | |
| (*a*) Cells in 4 groups, | *Dycticus.* |
| (*b*) Cells in 2 groups, distinguishable by comparison with neighboring cells, | *Aeschna.* |
| (*c*) Not so distinguishable, | *Tabanus.* |
| C. Cups unrecognizable even as rudiments, | *Hemiptera.* |

If such a superior neural function is indicated by the testimony and work of the earlier writers, it may well be asked whether recent neurological methods will bring out the structure of the hexapod brain as well as they have that of the other invertebrates and that of the vertebrates, and whether they will lend this view support. First, it may be noted that the physiological experiments of Binet ('94), which are those of

Faivre very much bettered, demonstrate that a hexapod may live for months without a brain, if the subæsophageal ganglion, or better, ventro-cerebron, is left intact, just as a vertebrate may live without its cerebrum. Faivre long ago showed that this ventro-cerebron is the seat of the power of co-ordination of the muscular movements of the body. Binet has shown that the brain is the seat of the power directing these movements. A debrainedhexapod will eat when food is placed beneath its palpi, but it cannot go to its food even though the latter be but a very small space removed from its course or position. Whether the insect would be able to do so if the mushroom bodies only were destroyed, and the antennal lobes, optic lobes, and the rest of the brain were left intact, is a question that yet remains to be answered. In Binet's experiments neither olfactory nor visual stimuli can be transformed into motor impulses. Were it possible for them to be so transformed, my studies to be noted in a moment cause me to think that Binet's results would be very materially altered.

Now, as to my studies. During the winter just past with no little patience I endeavored to apply the bichromate of silver method to a study of the brain and general nervous system of the common honey bee, the more detailed result of a portion of which will be published a little later. The endeavor was rewarded by a considerable degree of success, the main facts being determined, though there are many details left for future studies. Others have tried to employ the same general method, but owing to a lack of proper store of patience or to their setting about the task wrongly have failed. Among them must be counted Binet ('94), with whom, however, there seems to be a defect in the conception of both the Golgi and the Erlich methods. For he sets the former aside as inconstant, uses the latter, without, however, apparently obtaining any very good results. He complains that preparations by the Erlich method (and the Golgi method might be included) leave out many details, and never seems to think that a sufficient number of preparations will supply those details and thus allow the whole to be determined. This is the more unfortunate, since his dependence upon the old methods has led him to give detailed

importance to phenomena that are relatively unimportant, and has resulted in a somewhat misty conception of the structure of the hexapod ventral nervous system.

One of the very first things that an impregnation of bee brains with bichromate of silver enabled me to make out was the structure of the mushroom bodies with their cells. These cells stand out in sharp contrast to all other nerve cells known, though they recall to some extent the cells of Purkinje in the higher mammals. Each of the cells contained within the fibrillar cup seeds a nerve process into the later, where it breaks up into a profusely arborescent system of brahchlets, which often appear with fine, short, lateral processes, such as are characteristic of the dendrites of some mammalian nerve cells. Just before entering the fibrillar substance a fine branch is given off that travels along the inner surface of the cup along with others of the same nature, forming a small bundle to the stalk of the mushroom body, down which it continues until it reaches the origin of the anterior and the inner roots mentioned at the beginning of the paper. Here it branches, one branch continuing straight on to the end of the anterior root, while the other passes to the end of the inner root. Throughout its whole course the fiber and its two branches are very fine. Nearly the whole stalk and nearly the whole of each root is made up of these straight parallel fibers coming from the cells within the cup of the mushroom bodies. What other fibers there are enter these bodies from the side, and branch between the straight fibers very much as the dendrites of the cells of Purkinje branch among the parallel fine fibers from the cells of the granular layer in the mammalian cerebellum. These fibers are of the nature of association fibers.

From the olfactory or antennal lobe, from the optic ganglia there are tracts of fibers that finally enter the cups of the mushroom bodies as shown by Viallanes and by my studies with the Golgi method and also with a Formol-copper-hæmatoxylin method of staining. Besides these tracts the Golgi method has enabled me to make out another tract, unknown before, passing down the hinder side of the brain from the cups to the region above the œsophagus, where it bends forwards and comes in

contact with fibers from the ventral cord, which exists, although Binet was unable to discover any "growth of fibers connecting the cord with the brain."

The fibers entering the cups from the antennal lobe, the optic ganglia, and the ventral region, spread out and branch among the arborescent endings of the mushroom body cells.

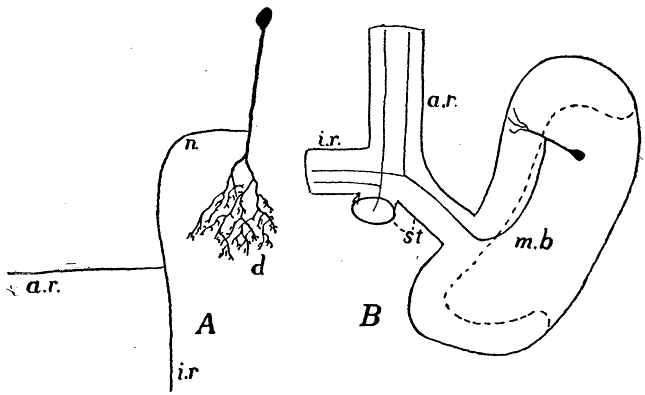


Fig. .—A. An "intellective" cell from the mushroom body. n, neurite; d. dendrite; a.r., anterior branch of the neurite; i.r., inner branch of the neurite. B. Mushroom body of right side from above. The outer one, m.b, viewed in section; the inner one is cut off, leaving the stump of the stalk st. a.r., anterior root; i.r., inner root; m.b., cup.

The fibers branching among the parallel fibers of the roots and the stalk lead off to lower parts of the brain, connecting with efferent or motor fibers, or with secondary association fibers, that in their turn make such connections. This portion of the circuit has not been perfectly made out, though there seems to be sufficient data to warrant the assumption just made.

Such fibers existing as described there is then a complete circuit for sensory stimuli from the various parts of the body to the cells of the mushroom bodies. The dendritic or arborescent branches of these cells take them up and pass them on out along the parallel fibers or neurites in the roots of the mushroom bodies as motor or other efferent impulses.

This, however, is not all. For there are numerous fibers evident in my preparations, the full courses of which I have not been thus far able to determine, but which are so

situated as to warrant the inference that they may act as association fibers between the afferent fibers from the antennæ, optic ganglia, and ventral system and the afferent fibers. There is then a possibility of a stimulus entering the brain and passing out as a motor impulse without going into the circuit of the fibers of the mushroom bodies, or, in other words, a possibility of what may be compared to reflex action in higher animals.

It appears then that the supposition of Dujardin is well supported by the finer structure of the hexapod brain. For it is evident from the details known since the publication of Flögel's paper, that the cells composing the mushroom bodies have been very highly differentiated in some of the hexapods, and this in just those forms living the most complex lives. No such bodies are to be found in the lower forms. I have never seen them, nor any indication of them, in the Thysanura, Chilopoda,[2] Scolopendrella, the Pauropoda and other Myriapoda, nor in any of the Crustacea that I have thus far examined. Without doubt an application of the Golgi or methylen blue methods would reveal elements in some these forms that might be compared with the cells of the mushroom bodies; but they would probably be found not so completely differentiated from other fibers as they are in the honey bee and other Hymenoptera. It may be mentioned that one does not recognize such cells in the cray-fish and the crab as figured by Retzius and Bethe. And it scarcely need be said that no such elements are shown in Retzius' figure of the brain of *Nereis*.

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[2] St.-Remy ('90) describes mushroom bodies as occuring in *Scutigera*, which if homologous with the mushroom bodies of Hexapoda, is in accordance with Dujardin view.

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